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LARVAL SUPPLY TO QUEEN CONCH NURSERIES: RELATIONSHIPS WITH RECRUITMENT PROCESS AND POPULATION SIZE IN FLORIDA AND THE BAHAMAS

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ABSTRACT Surveys were made for larvae of the commercially important gastropod *Strombus gigas* Linne (queen conch) over two spawning seasons in two island chains of the northwestern subtropical Atlantic, the Florida Keys (United States) and the Exuma Cays (Bahamas). Size-frequency distribution of veligers in the Florida Keys was characterized by two distinct modes representing newly hatched larvae (<500 μm in shell length) and larvae near metamorphosis (>900 μm) in approximately equal numbers, with virtually no mid-size larvae. The Florida Keys have a very small spawning stock, yet densities of late-stage larvae were nearly as high as those in the Exuma Cays, where spawning stocks are large. Late-stage larvae in the Keys appear to be derived from distant spawning stocks, probably in Cuba or the western Caribbean Sea. In contrast, only 1% of the larvae in the Exuma Cays were late stages and the juvenile populations appear to depend on local spawning and recruitment. The sizes of juvenile populations were positively correlated with the mean density of late-stage larvae in both the Florida Keys ($r = 0.881$) and the Exuma Cays ($r = 0.759$), indicating the significance of larval supply in determining benthic recruitment on the local scale. The slope of the linear relationship between larval supply and juvenile population size, however, was much higher in the Exuma Cays nurseries than in Florida, suggesting important regional differences in settlement and postsettlement processes. Recruitment of benthic fauna with pelagic larvae must be considered in terms of metapopulation dynamics and both presettlement and postsettlement processes.

KEY WORDS: Bahamas, distribution, Florida, larval transport, length-frequency, *Strombus gigas*

INTRODUCTION

A large proportion of benthic marine animals have "complex life cycles" (sensu Roughgarden et al. 1988) involving pelagic eggs or larvae with high potential for dispersal as well as loss to stochastic, density-independent processes during larval development. Connell (1985) predicted that population sizes of benthic animals would be positively correlated with recruitment density where recruitment rate is low and that density-dependent mortality would rapidly destroy a direct relationship between larval settlement and subsequent recruitment where recruitment rate is high. Numerous studies with fishes (Sale et al. 1984, Victor 1986, Doherty 1987) and invertebrates (Keough 1984, Connell 1985, Gaines et al. 1985, Sutherland 1987, Roughgarden et al. 1988) have examined the relationship between settlement and subsequent population size. Others have made empirical analyses of the relationship between larval supply and settlement and/or recruitment (Yoshioka 1982, Wethey 1984, Gaines et al. 1985, Lipcius et al. 1990, Minchinton and Scheibling 1991, Milicich et al. 1992, Peterson and Summerson 1992, Doherty and Fowler 1994).

The large gastropod *Strombus gigas* Linne (queen conch) forms the basis for one of the most important fisheries of the Caribbean region, with a total annual value of approximately $40 million US between 1988 and 1991 (Appeldoorn 1994). However, queen conch stocks have declined throughout the region over the past 10–20 y, and various forms of catch and size limits have been imposed in most nations (Appeldoorn et al. 1987, Berg and Olsen 1989, Appeldoorn 1994). International trade in conch is now monitored by the Convention on International Trade of Endangered Species (CITES) with the hope of ensuring the species' survival. Despite complete closure of the fishery in the United States in 1985, queen conch stocks have shown little sign of recovery (Berg and Glazer 1995). This lack of recovery is poorly understood, in part because of limited knowledge of early life history, larval abundance, and recruitment processes. The ecology of the juvenile and adult queen conch is relatively well studied (Randall 1964, Weil and Laughlin 1984, Iversen et al. 1987, Stoner and Waite 1990, Stoner and Sandt 1992, Stoner et al. 1995); however, detailed larval descriptions for identifying the larvae of the different *Strombus* species (Davis et al. 1993) and the first analyses of veliger abundance (Stoner et al. 1992, Posada and Appeldoorn 1994, Stoner et al. 1994) have appeared only recently. The recruitment problem is compounded by the fact that queen conch larvae spend ~3 wk in the water column and may drift hundreds of kilometers from parental stocks before settling to the benthos (Davis et al. 1993). As a result, many local populations are probably replenished from distant sources, and stock management for queen conch is a multinational problem (Berg and Olsen 1989). Biochemical evidence suggests a high degree of gene flow among Caribbean populations (Mitton et al. 1989, Campton et al. 1992).

This study was conducted to compare the abundance and size frequency of queen conch larvae within and between two geographically distinct regions. At both sites, collections were made in nursery areas with the broadest possible range of juvenile population size to examine the relationship between larval supply and spatial variation in recruitment. Analyses were made in the Florida

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Keys (United States), where populations have been heavily overfished (Glazer and Berg 1994), and in the Exuma Cays (Bahamas), where conch populations were large and relatively stable (Stoner and Sandt 1992, Stoner and Schwarte 1994, Stoner et al. 1996). Differences in the benthic populations both within and between regions are discussed in terms of potential sources of larval recruitment, long-term juvenile population size, stock recovery, and management strategy.

METHODS

Stations in Florida

Stations in the Florida Keys were chosen on the basis of long-term data for historically important conch nursery grounds in the middle and lower Florida Keys (Glazer and Berg 1994, our unpubl. data). Two stations were in nearshore locations (Tingler's Island [TI] and Big Pine Key [BP]; Fig. 1) that had small, ephemeral populations of juveniles (Table 1). These sites were ~1.5 m deep at mean low water (MLW), and the bottom was a mixture of macroalgae, sponges, sand, and patches of seagrass (primarily *Thalassia testudinum* Konig). Two more stations were located on nursery grounds associated with shoal areas along the Florida Keys coral-reef tract, which lies ~10 km offshore and to the south of the islands. These areas, Delta Shoal and Looe Key National Marine Sanctuary, typically support several hundred to a few thousand conch (Table 1). Delta Shoal is a shallow, coral-rubble area covered with macroalgae, small corals, and patches of sand. Delta Shoal station 1 (DS1) was located in the backreef area along the northern edge of the shoal over a 1.5-m-deep platform of mixed seagrass, rock, algae and sponges. Station 2 (DS2) was ~0.5 km offshore from the shoal, where depth increased rapidly from 20 to 30 m. Looe Key is composed of a very shallow coral-reef tract running east to west, with shallow rubble shoals reaching north from the ends of the reef. Station 1 (LK1) was behind the reef and between the shoals, where there is a shallow sand- and seagrass-covered flat. Station 2 (LK2) was ~0.5 km offshore in depths of 20–30 m. At both Delta Shoal and Looe Key, juvenile conch are found consistently on algae-covered rubble and seagrass in shallow water. Adults are found on the reef flat at Looe Key and in the deep areas surrounding the reefs and shoals at both sites. Spawning occurs principally in these deeper habitats and has not been observed north of Hawk Channel.

Stations in the Bahamas

Five stations were chosen on the basis of long-term data from the Lee Stocking Island area in the southern Exuma Cays (Stoner et al. 1994, Stoner et al. 1995, our unpubl. data) (Fig. 1). Stations at Children's Bay Cay (CBC), Shark Rock (SR), Tug Boat Rock (TBR), and Neighbor Cay (NBC) were all on the shallow Great Bahama Bank to the west of the Exuma Cays (leeward in prevailing summer winds). The fifth station was on the windward island shelf of Lee Stocking Island in a cove off of Charlie's Beach (CHB). As is typical of large nursery grounds in the Exuma Cays, CBC and SR are characterized by moderate-density seagrass (*T. testudinum*), shallow depth (3.0 m at MLW), and strong tidal currents. Both have large aggregations of 70,000 or more juvenile conch in most years (Table 1). TBR, NBC, and CHB have smaller, more ephemeral populations, with TBR being the largest and most consistent (7,000–50,000 individuals), and CHB and NBC rarely having more than 200–2,000 conch (Table 1). TBR is

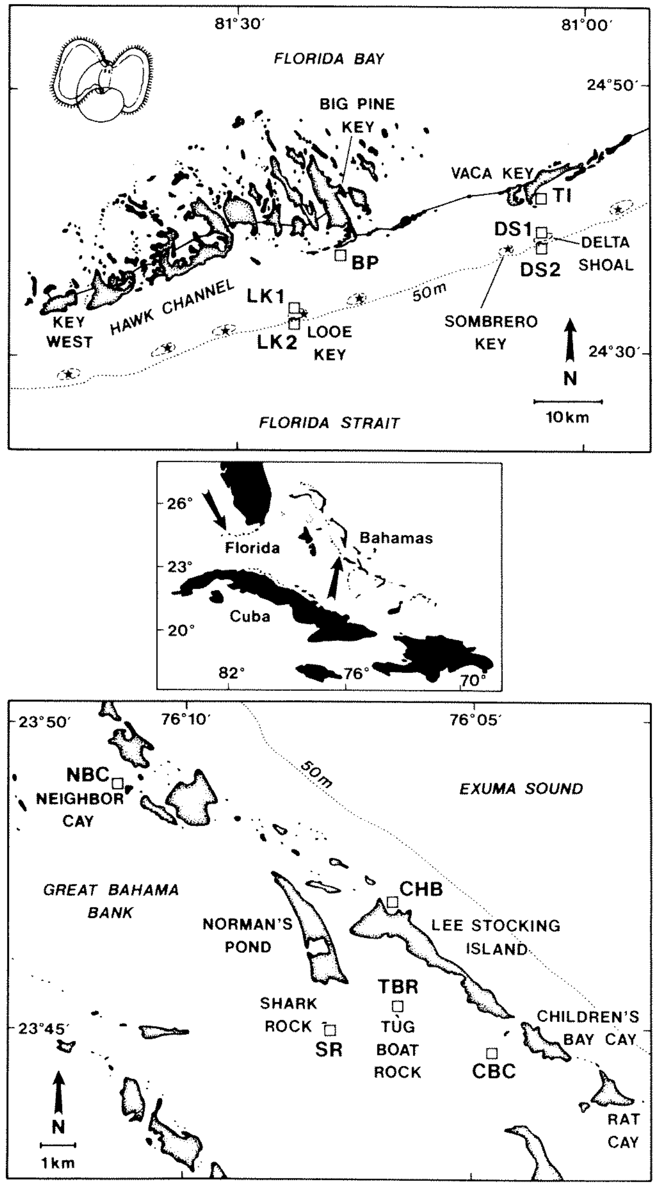

Figure 1. Location of veliger-sampling sites in the Florida Keys (top) and Exuma Cays, Bahamas (bottom). Arrows in the center map show the general locations of the two study sites. Note the scale differences for the Florida and Exuma maps.

2.0 m deep and has sparse to medium-density seagrass and strong tidal currents. Where plankton tows were made in the cove at CHB, depth is 1.5–2.5 m and the bottom is a mixture of bare sand and patches of sparse to dense *T. testudinum*, detritus, and drift algae. Conch at NBC inhabit a depth range from immediately subtidal to approximately 2.0 m in depth in an area grading from a bare sand beach to a sparsely vegetated seagrass bed (Sandt and Stoner 1993). Adult density and spawning frequency are highest in depths of 10–18 m on the island shelf to the east of the Exuma Cays (Stoner and Sandt 1992, Stoner and Schwarte 1994). Spawning is relatively infrequent in bank habitats to the west of the Exuma Cays.

Plankton Collections

Plankton samples were collected with simple conical nets (0.5 m in diameter, 2.5 m in length, 202-μm-pore-size mesh). Repli-

TABLE 1.

Estimates of Juvenile Population Size of Queen Conch at Nine Nurseries in the Florida Keys and Exuma Cays, Bahamas, 1988–1994.

	Florida Keys				Exuma Cays				
Year	Tingler's Island (TI)	Delta Shoal (DS1)	Big Pine Key (BP)	Looe Key (LK1)	Children's Bay Cay (CBC)	Tugboat Rock (TBR)	Shark Rock (SR)	Charlie's Beach (CHB)	Neighbor Cay (NBC)
1988	600	—	13,084	—	—	—	—	—	2,500
1989	1,012	—	1,716	—	—	—	—	—	6,000
1990	170	14,400	78	810	110,000	50,000	220,000	—	—
1991	0	13,800	0	6,890	10,000	500	162,000	281	—
1992	536	845	3,920	722	90,000	7,000	70,000	229	—
1993	228	1,830	368	2,116	145,900	47,600	84,900	50	100
1994	70	1,282	0	2,504	165,600	100,700	85,700	0	0
Mean	374	6,431	2,738	2,608	104,300	41,160	124,520	140	2,150

Population size at stations TI and BP were determined by standard tag and recapture methods (Glazer and Berg 1992), whereas the larger, more dense populations in the Florida Keys (DS1 and LK1) were surveyed by the use of standardized belt-transect methods (Glazer and Berg 1994). The numbers of juveniles in the largest populations (CBC, SR, and TBR) were estimated by measuring the density of conch in highly replicated quadrats within multiple sectors of the aggregation, which were mapped with the aid of the global positioning system (Stoner and Ray 1993, Stoner et al. 1994).

cate tows ($\sim$1.0 m $\cdot$ sec^{-1}) were made at each station and sample date near the water surface. Surface sampling was appropriate because queen conch veligers are photopositive (Barile et al. 1994) and most abundant near the surface under relatively smooth surface conditions (Stoner and Davis 1997b). In the Florida Keys, sampling was restricted to mid-day periods when wave height was <0.5 m. In the Exuma Cays, where the nurseries are subject to strong tidal currents, sampling was restricted as described above and confined to time periods 2 h before and 1 h after the high tide. Stoner and Davis (1997a) have shown that the highest concentrations of veligers pass through the inlets at mid-flood tide. We assumed, therefore, that maximum densities at the nurseries would occur close to the high tide. Tow times varied according to the concentration of plankton on the sampling date but averaged 15 min each. Tow volume was determined with a calibrated General Oceanics flow meter suspended in the mouth of the net. Nets were deployed by hand from small boats (<8 m). Plankton samples were preserved in a buffered 5% formalin-seawater mixture.

At both sites, sampling was conducted between late May and late September in 1992 and 1993, seasonal periods that spanned the primary reproductive season at Lee Stocking Island (Stoner et al. 1992) and in the Florida Keys (Glazer, pers. observ.). In 1992, samples were collected every 2 wk at the Florida stations for a total of eight sets of plankton. At the Exuma stations, samples were collected every 9 d, yielding 13 sets. In 1993, the sampling effort was increased to 12 collections in the Florida Keys and 14 collections near Lee Stocking Island. On each sampling date, observations were made on wave height and direction, wind speed and direction, and surface-water temperature.

In the laboratory, plankton samples were rinsed on a 180-μm-pore-size mesh screen and sorted for veligers of *Strombus* spp. with the aid of a dissecting microscope. Even the smallest veligers of *Strombus gigas, Strombus costatus,* and *Strombus raninus* can be distinguished by use of the descriptions of Davis et al. (1993). These were identified to species, counted, and measured for maximum shell length (SL). Patterns of abundance for *S. gigas* were analyzed in terms of numbers of veligers per unit volume of water sampled (veligers $\cdot$ 100 m^{-3}) for the total number of veligers and by size class. Classes used were: early-stage (<500 μm SL), mid-size (500–900 μm), and late-stage veligers (>900 μm), most of which were metamorphically competent. In an open system, larvae of different sizes may have different sources and size-specific density data are useful in interpreting larval production and transport processes. For example, early-stage conch veligers are only a few days old (Davis et al. 1993) and reflect local larval production, whereas late-stage veligers may have a source in more distant reproductive populations.

Juvenile Population Size

To test for a relationship between the supply of larvae to nurseries and the subsequent benthic population, regression analysis was performed using the mean seasonal density of late-stage veligers as the independent variable for each station and the estimated total number of juveniles in the population the following year as the dependent variable. That is, 1992 veliger data were paired with 1993 data for juveniles, and 1993 veliger data were paired with 1994 data for juveniles. Juveniles were predominantly 1-y-old conch, 80–120 mm SL. The methods used to estimate juvenile population size (see Table 1) have been described in detail for both the Florida Keys (Glazer and Berg 1992, Glazer and Berg 1994) and the Exuma Cays (Stoner and Ray 1993; Stoner et al. 1994).

RESULTS

Spatial Variation in Veliger and Size Frequency

In 1992, only 209 queen conch veligers were collected in all 96 tows in Florida, whereas over 3,900 were collected in 130 tows in the Exuma Cays (Table 2). Total numbers collected in the two geographic areas were relatively similar in 1993 (2,300–2,700); however, most of the 2,600 veligers at LK1 were newly hatched individuals collected on just one date. In Florida, the highest mean veliger concentration occurred at LK1 during both 1992 (9.1 veligers $\cdot$ 100 m^{-3}) and 1993 (140 veligers $\cdot$ 100 m^{-3}) (Table 2). Over the 2-y survey period, only one queen conch veliger was collected at TI, and only two were collected at BP. Densities of conch veligers were generally higher in the Exuma Cays than in the Florida Keys. Densities near the largest populations at SR, CBC, and TBC were 15–33 veligers $\cdot$ 100 m^{-3} in 1992 and 12–

TABLE 2.

Counts and Density of Queen Conch Veligers (All Stages) Collected in the Florida Keys and Exuma Cays, Bahamas, May Through September 1992 and 1993.

	1992		1993	
Site and Station	No. of Veligers Collected	Veliger Density (no. · 100 m^{-3})	No. of Veligers Collected	Veliger Density (no. · 100 m^{-3})
Florida Keys	16 tows		24 tows	
Tingler's Island (TI)	0	0 ± 0	1	0.06 ± 0.19
Delta Shoal 1 (DS1)	11	0.86 ± 1.77	71	2.40 ± 6.80
Delta Shoal 2 (DS2)	29	2.60 ± 5.50	ND	ND
Big Pine Key (BP)	1	0.07 ± 0.27	1	0.07 ± 0.22
Looe Key 1 (LK1)	144	9.10 ± 19.8	2,637	140 ± 443
Looe Key 2 (LK2)	24	1.10 ± 1.90	ND	ND
Total	209		2,710	
Exuma Cays	26 tows		28 tows	
Children's Bay Cay (CBC)	939	17.8 ± 14.7	942	12.5 ± 18.0
Tugboat Rock (TBR)	799	15.6 ± 13.7	278	3.57 ± 6.60
Shark Rock (SR)	1,576	32.5 ± 34.8	1,001	12.5 ± 9.7
Charlie's Beach (CHB)	123	2.30 ± 2.70	ND	ND
Neighbor Cay (NBC)	494	9.80 ± 9.40	136	1.70 ± 3.30
Total	3,914		2,357	

Density values are mean ± standard deviation. The number of tows made at each station is shown for each of the 2 y. ND, not determined.

36 veligers · 100 m^{-3} in 1993 (Table 2). Densities near the smaller, more ephemeral juvenile populations were 1.7–9.7 veligers · 100 m^{-3}.

All of the queen conch veligers collected in the Florida Keys were either very small, newly hatched individuals (most were <400 μm SL) or late-stage larvae (>900 μm SL). There were no intermediate stages. Nevertheless, two types of size-frequency distribution were observed at Looe Key and Delta Shoal (Fig. 2). Directly over the nurseries (LK1 and DS1), most of the larvae collected were early stages, probably just 1–4 d old. Conversely, no larvae <1.0 mm SL were collected at offshore station LK2, and only three individuals <1.0 mm were collected at DS2. The differences were highly significant for both station pairs (Kolmogorov-Smirnov tests, $p < 0.01$).

Size-frequency distributions for veligers collected in the Exuma Cays were dominated by early-stage larvae (Fig. 3). At all five stations, small veligers (<500 μm SL) comprised >93% of the total numbers; however, mid- and late-stage veligers were also collected at all stations.

Occurrence of Precompetent Veligers

Densities of early-stage larvae were relatively high (near 25 veligers · 100 m^{-3}) at Exuma Cays stations SR, CBC, and TBR throughout the spawning season in 1992 (Fig. 4), with strong maxima (>100 veligers · 100 m^{-3}) occurring at SR in June and late August. Although larval densities were obviously lower in 1993 than in 1992, densities of early stages were never zero at these three nurseries with large populations of juvenile conch. Among the Exuma Cays stations with low numbers of juvenile conch, early-stage veligers were constantly present at NBC in 1992, but they were present in only 4 of 13 collections made in 1993. At CHB, concentrations were low, but positive, on all but two dates with no veligers collected. None of the Exuma Cays stations showed an obvious temporal pattern in veliger density during the spawning seasons of 1992 and 1993.

Among the Florida stations, early-stage larvae were sufficiently abundant to warrant plotting only at LK1 (Fig. 4). Densities were erratic, with high concentrations interspersed among zero values throughout both 1992 (50% zeros) and 1993 (33% zeros). Eighty-eight percent of all of the conch veligers collected at this station in 2 y were very recently hatched larvae (<400 μm SL) collected on 22 July 1993. Early-stage larvae were never collected at LK2. At DS1, early stages were collected on 4 of 20 sampling dates, with only one density estimate >1 veliger · 100 m^{-3} (24.8), occurring on 8 July 1993. At DS2, early-stage veligers were collected on only two dates in 1992, with values ≤0.7 veligers · 100 m^{-3}.

Density of early-stage larvae showed no particular association with wind direction or speed except that none were collected on the relatively few dates (three dates at Looe Key, one date at Delta Shoal) when wind velocity exceeded 7.3 m · sec^{-1} (15 knots). The very high concentration of newly hatched larvae estimated for LK1 in July 1993 was associated with calm conditions and the highest recorded temperature for the season (32°C).

Whereas no mid-stage conch veligers were collected in the Florida Keys, they were present in 56% of the samples at CBC and 44% of the samples at SR. Densities were much lower than those for early-stage larvae, typically <1–2 veligers · 100 m^{-3}, with maxima occurring irregularly (Fig. 5). Densities of mid-stage larvae were never >1 veliger · 100 m^{-3} at TBR, NBC, and CHB. At all of the stations, mid-stage larvae were relatively uncommon before mid-June in both 1992 and 1993, probably reflecting the beginning of the reproductive season and the subsequent growth of the larvae. As with early-stage larvae, mid-stage veligers were more abundant at SR in 1992 than in 1993. At CBC, mid-stage larvae were more abundant in 1993 than in 1992, but densities were erratic in all cases.

Occurrence of Competent Veligers

Concentrations of late-stage larvae, all of which were competent or near competent, are particularly relevant to benthic recruitment in the nursery habitats; therefore, these were considered sep-

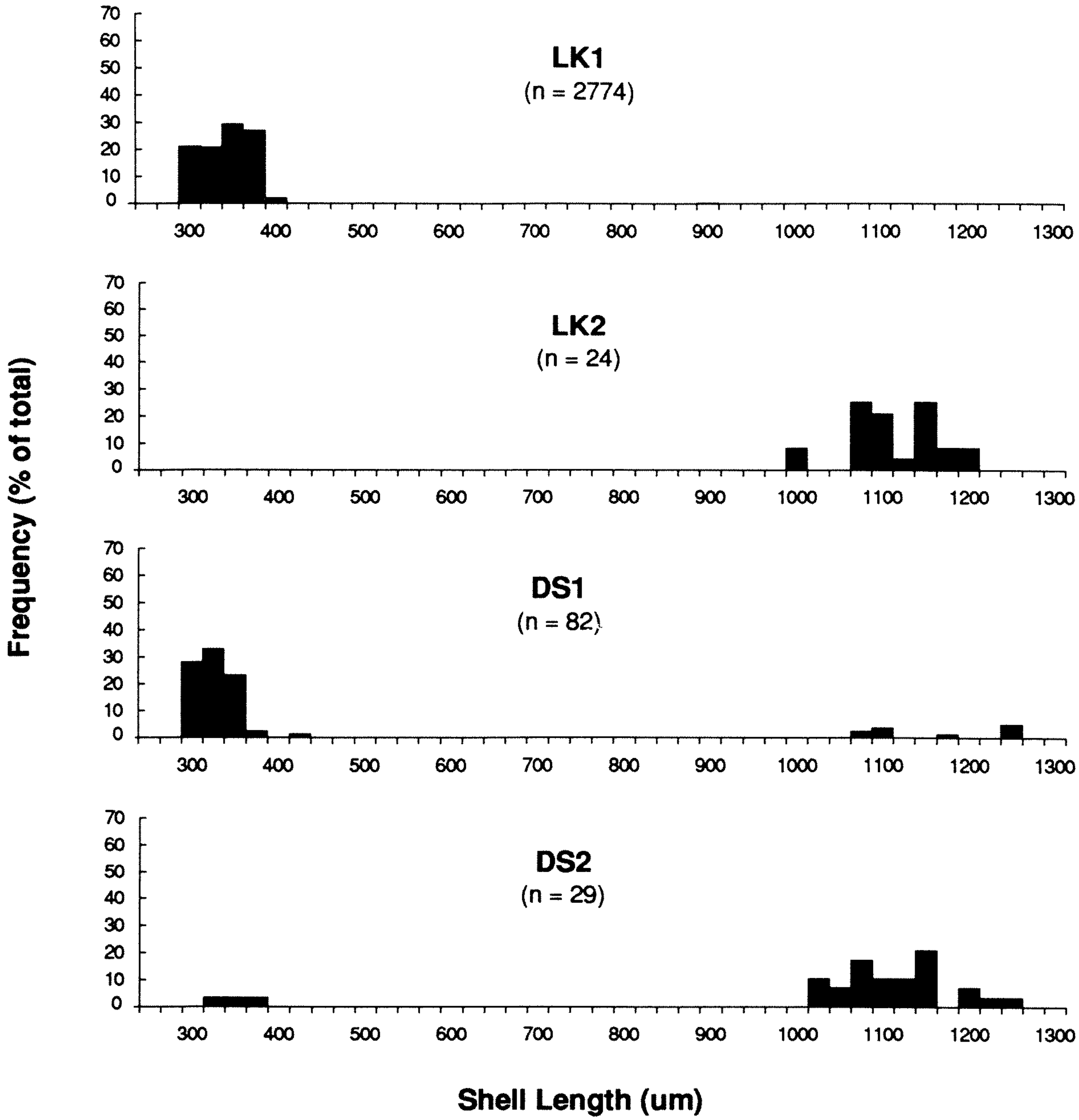

Figure 2. Length-frequency distribution of queen conch veligers at four stations in the Florida Keys in 1992 and 1993. The total number of larvae shown for station LK1 is slightly less than that reported in Table 2 (2,781) because some shells were damaged and not measured.

arately (Table 3; Fig. 6). The highest concentrations of late-stage larvae occurred in 1992, at the offshore Florida stations DS2 (1.34 veligers · 100 m^{-3}) and LK2 (0.85 veligers · 100 m^{-3}), where late stages comprised most of the larvae (Fig. 2). Among the nursery sites, the densities of late-stage larvae ranged from zero at stations characterized by very small populations of juveniles, TI and BP, to 0.34 veligers · 100 m^{-3} at DS1 in 1993 (Table 3). Mean concentrations were relatively consistent between 1992 and 1993 at the Florida nurseries; however, the frequency of occurrence of late-stage veligers was lower in the second year. The highest concentrations of late-stage veligers at nursery sites LK1 and DS1 were associated with onshore winds from the south. Conversely, at all four stations near the reef tract (at Delta Shoal and Looe Key), larval densities were zero whenever the wind was north of east (<90–110° true), suggesting that the larvae were transported on and off the shelf with the surface layer.

In general, the mean densities of late-stage larvae at the Exuma Cays stations were not much higher than those in the Florida Keys (Table 3), despite very large differences in total larval densities (Table 2). The highest density for one date was 5.9 veligers · 100 m^{-3} at CBC in August 1993; however, densities >2 veligers · 100 m^{-3} were uncommon (Fig. 6). Late-stage larvae occurred sporadically, with less than half of the sampling dates yielding late-stage larvae (Table 3), and there was no concordance in the abundance patterns at SR and CBC, which lie in adjacent tidal flow fields and are separated by just 7 km. Consistent with the pattern observed for early- and mid-stage larvae, late-stage larvae were more abundant at SR in 1992 than in 1993.

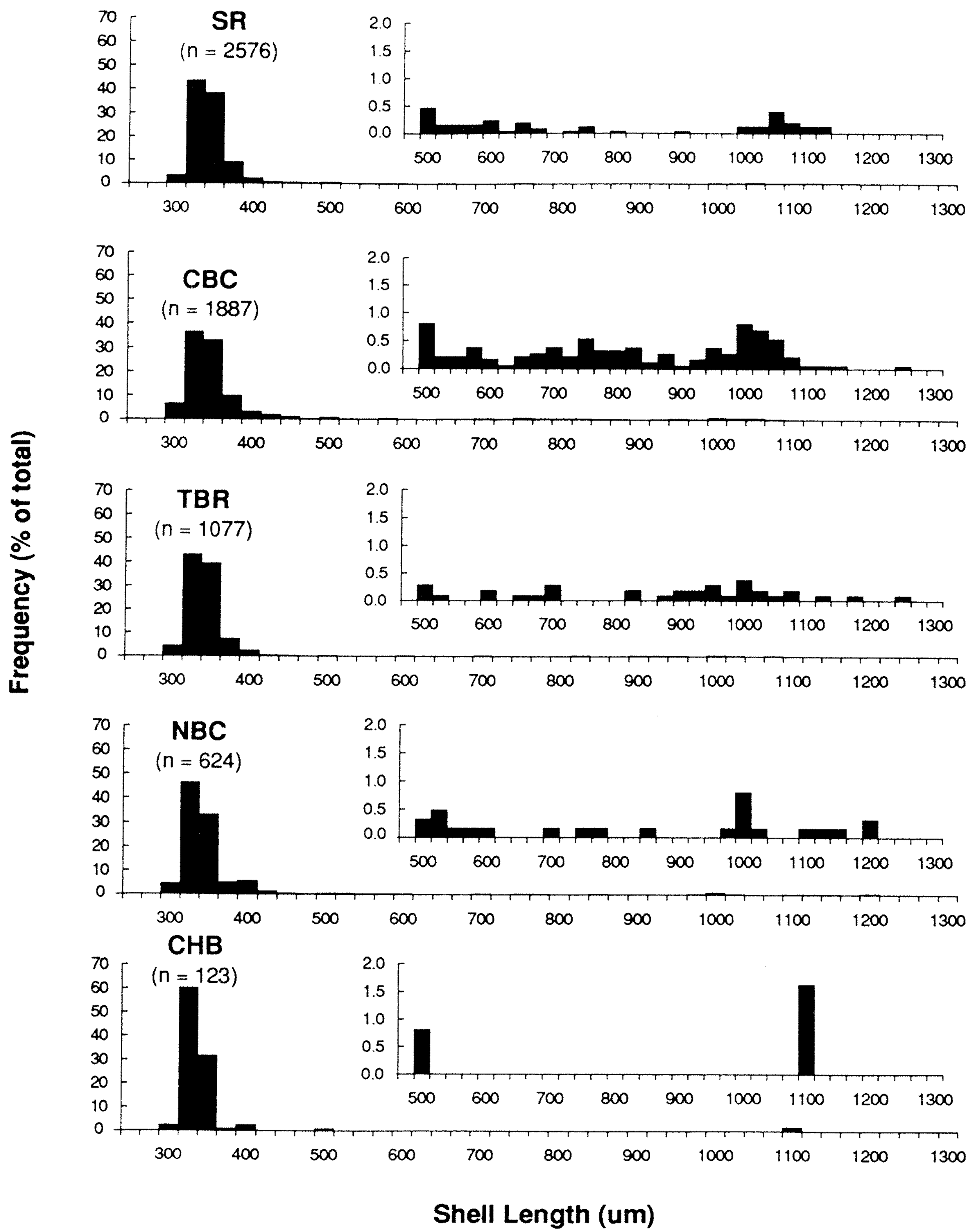

Figure 3. Length-frequency distribution of queen conch veligers at five stations in the Exuma Cays in 1992 and 1993. The frequency distributions of larvae >500 μm SL are shown in the insets. Note the scale difference on the y-axes. Small differences in the total numbers reported here and in Table 1 occur because some shells were damaged and not measured.

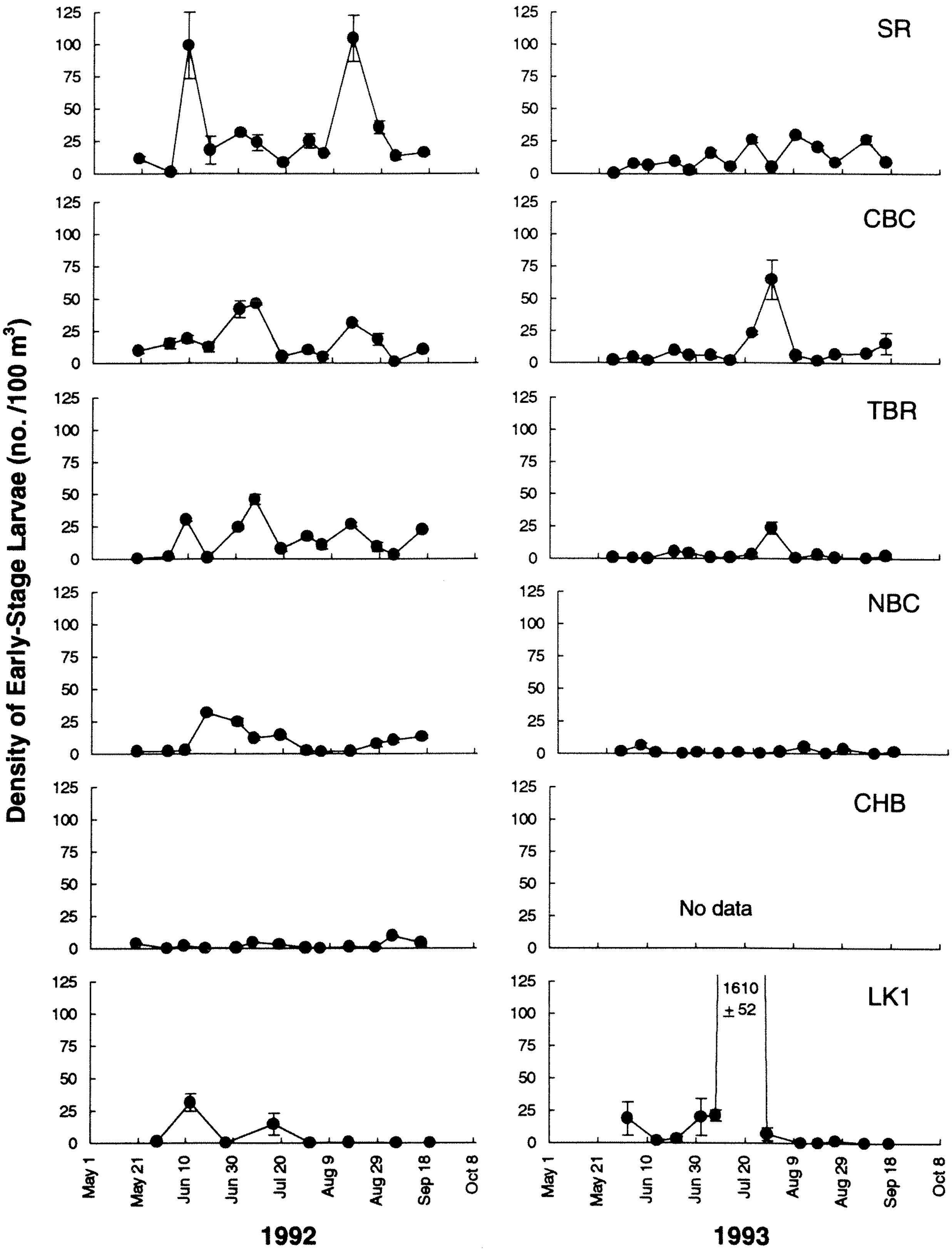

Figure 4. Density of newly hatched queen conch veligers (<500 μm SL) at five nurseries in the Exuma Cays, Bahamas, and at the Looe Key nursery (Florida Keys) in 1992 and 1993. Numbers of larvae collected at the other study sites were too low to plot. Values shown are mean ± standard error (n = 2).

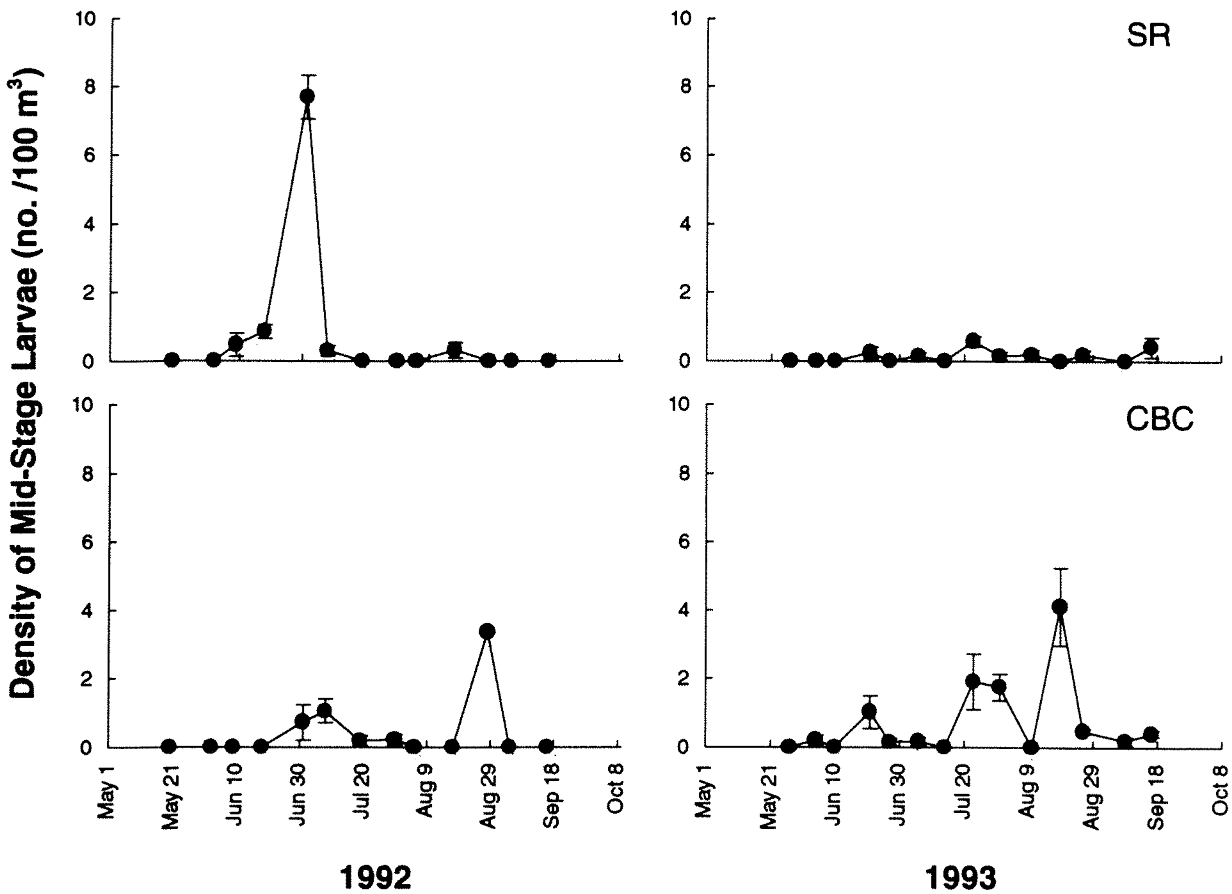

Figure 5. Density of mid-stage queen conch veligers (500–900 μm SL) at two nurseries in the Exuma Cays, Bahamas, in 1992 and 1993. Numbers of larvae collected at the other study sites were too low to plot. Values shown are mean ± standard error (n = 2).

TABLE 3.

Counts and Density of Late-Stage Queen Conch Veligers Collected in the Florida Keys and Exuma Cays, Bahamas, May Through September 1992 and 1993.

Site and Station	1992 No. of Veligers Collected	1992 % of Collections With Veligers	1992 Veliger Density (no. · 100 m^{-3})	1993 No. of Veligers Collected	1993 % of Collections With Veligers	1993 Veliger Density (no. · 100 m^{-3})
Florida Keys	16 tows			24 tows		
Tingler's Island (TI)	0	0	0 ± 0	0	0	0 ± 0
Delta Shoal 1 (DS1)	6	50	0.28 ± 0.34	5	8	0.34 ± 1.04
Delta Shoal 2 (DS2)	26	50	1.34 ± 1.82	ND	ND	ND
Big Pine Key (BP)	0	0	0 ± 0	0	0	0 ± 0
Looe Key 1 (LK1)	2	25	0.10 ± 0.21	5	17	0.16 ± 0.56
Looe Key 2 (LK2)	24	38	0.85 ± 1.65	ND	ND	ND
Total	58			10		
Exuma Cays	26 tows			28 tows		
Children's Bay Cay (CBC)	8	15	0.32 ± 0.79	54	50	0.55 ± 1.55
Tugboat Rock (TBR)	6	15	0.13 ± 0.38	14	36	0.21 ± 0.34
Shark Rock (SR)	23	39	0.52 ± 1.45	6	29	0.08 ± 0.14
Charlie's Beach (CHB)	2	8	0.06 ± 0.23	ND	ND	ND
Neighbor Cay (NBC)	2	15	0.04 ± 0.09	10	43	0.11 ± 0.17
Total	41			84		

Density values are mean ± standard deviation. The number of tows made at each station is shown for each of the 2 y. ND, not determined.

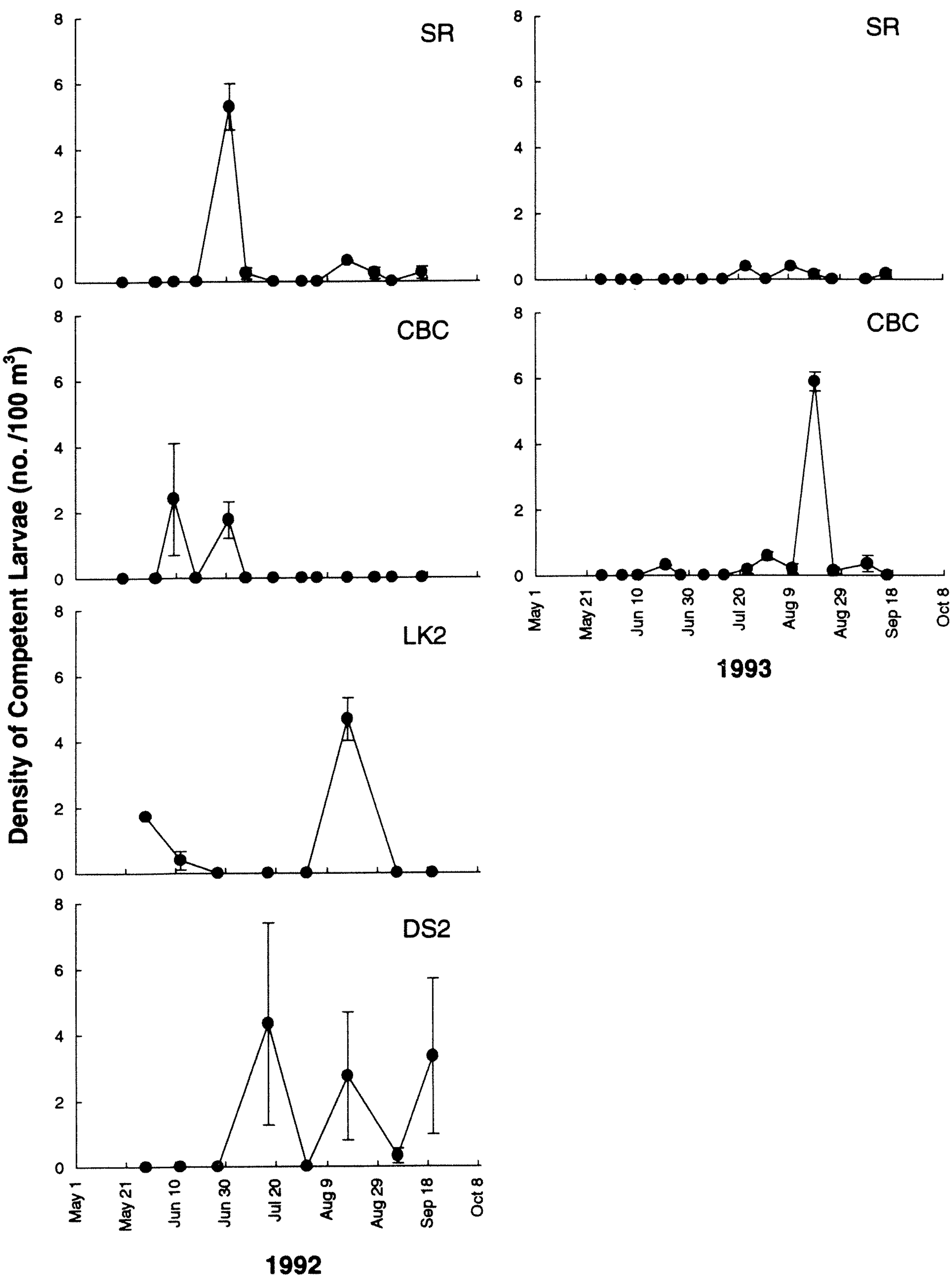

Figure 6. Density of late-stage queen conch veligers (>900 μm SL) at two stations in the Exuma Cays and at two stations in the Florida Keys in 1992 and 1993. Relatively few late-stage larvae were collected at the other sampling stations (see Table 3). Values shown are mean ± standard error (n = 2).

Relationships Between Veligers and Juvenile Population Size

Two general observations can be made about the relationship between the density of veligers and juvenile populations at the study sites. First, veliger densities were consistently low (Table 2) at stations with ephemeral or small juvenile populations, such as TI and BP in the Florida Keys and CHB in the Exuma Cays (Table 1). Second, in the Exuma Cays, veligers were always present, and density maxima were high at nurseries where there were consistently large aggregations of juvenile conch (i.e., CBC and SR). Similarly, the highest larval densities in the Florida Keys occurred at LK1 and DS1, where juveniles were most abundant.

There was a close, positive correlation between larval supply (mean seasonal density of late-stage conch veligers) and the size of the juvenile population 1 y later, both in the Exuma Cays ($r = 0.759$; $p = 0.018$) and in the Florida Keys ($r = 0.881$, $p = 0.004$) (Fig. 7). Analysis of covariance, however, indicated that the slopes of the regression lines for the two regions were different ($F_{(1,13)} = 5.061$; $p = 0.042$). It is clear from the plots (Fig. 7) that the slope for the Exuma Cays stations was much higher than that for the Florida Keys; the difference was >40 times. For example, a density of 0.3 late-stage veliger · 100 m^{-3} in the Florida Keys was associated with ~2,000 juvenile conch, whereas the same concentration of larvae in the Exuma Cays was associated with ~80,000 juveniles.

There was also a significant positive correlation between the abundance of juvenile conch in Florida nursery grounds and the percentage of plankton sampling dates (during the previous year) that yielded late-stage veligers ($r = 0.733$; $p = 0.039$). The correlation was not significant in the Exuma Cays ($r = 0.410$; $p = 0.273$).

DISCUSSION

Veliger Size Frequency and Probable Sources

Detailed length-frequency data for queen conch veligers generated in this study provide important insights into the different mechanisms of recruitment and sources of larvae for the two study areas. At all stations except the offshore non-nursery sites DS2 and LK2 in the Florida Keys, the majority of veligers were <500 μm SL. On the basis of growth curves provided by Davis et al. (1993), these small veligers were no more than 5–6 d old and must have had a local source. With the exception of one collection made in Looe Key National Marine Sanctuary in 1993, the density of newly hatched conch larvae was very low compared with the densities of similar sized veligers in the Exuma Cays, Bahamas. The difference relates to the abundance of spawners in the two areas. Adult conch in the Keys were seriously depleted by overfishing and have not recovered since fishing was ended in 1985 (Glazer unpubl. obs.). In 1992, there were only ~6,000 adult conch in the 200-km-long island chain of the Florida Keys from Carysfort Reef to Western Dry Rocks. Many of these adults were found in Looe Key National Marine Sanctuary, where the highest concentrations of early-stage veligers were collected in both 1992 and 1993.

In contrast with the low numbers of reproductive conch in the Florida Keys, densities of adults near Lee Stocking Island ranged from 2 to 88 individuals/ha in 1991, with an estimate of 89,000 adults in just a 12-km-long section of the island shelf (Stoner and Schwarte 1994). This provides a plausible explanation for the large numbers of early-stage larvae collected in the Exuma Cays compared with the low densities in Florida. An analogous relationship between the abundance of early-stage larvae and adult densities has been described for fished and unfished areas in the Exuma Cays island chain (Stoner and Ray, unpub. obs.).

Temporal variation in the densities of early-stage larvae is influenced by local spawning frequency, egg hatching, and physical factors such as sea surface conditions. The high abundance of newly hatched veligers at LK1 on 22 July 1993, for example, was associated with very warm water temperature (32°C), known to influence spawning (Stoner et al. 1992). Stoner and Davis (1997b) have shown that conch larval abundance in the upper water column is influenced by wave action, and calm conditions probably allowed conch larvae to accumulate both in the surface layer and in backreef areas such as that near Looe Key reef. However, it is impossible thus far to separate the effects of spawning, hatching, and larval behavior and transport on larval abundance patterns.

Densities of mid- and late-stage larvae are more relevant than those of early stages to the recruitment process. The complete lack of mid-size veligers in the Florida Keys and the high abundance of late-stage larvae relative to early stages, particularly in the offshore sites, indicate that the source for these late stages was probably not local. It is possible that the late-stage veligers were spawned in Florida and retained in gyres south of the Keys (Lee et al. 1992, Lee et al. in press). This retention mechanism has been hypothesized for lobsters in the genus *Scyllarus,* which have a 1- to 2-mo larval phase (Yeung and McGowan 1991); however, two lines of evidence indicate that the retention of conch larvae in the Florida Strait is unlikely. First, no intermediate-size larvae have ever been collected in the waters of the Florida Keys or Florida Strait (see below), and second, the densities of late-stage veligers were equal to or higher than those for early-stage larvae. Rates of mortality for queen conch larvae are unknown but assumed to be high.

Given distances, and average current patterns and velocities between the Yucatan Strait and the Florida Strait, coupled with the assumed age of veligers collected in the Florida Keys, it is most likely that late-stage veligers were transported from spawning populations in Cuba, Mexico, or Belize. Such a larval transport mech-

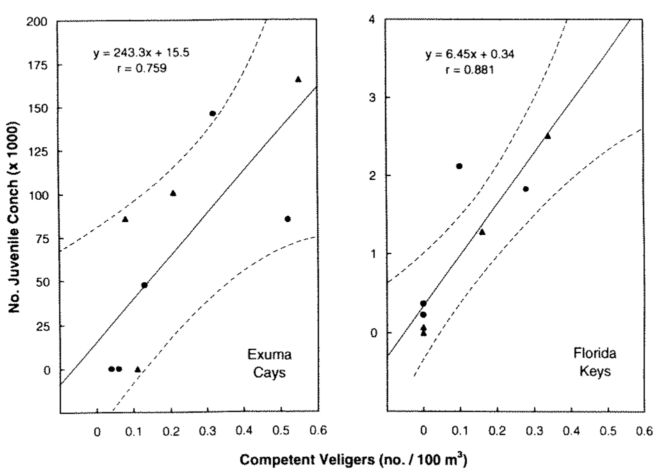

Figure 7. Relationship between the mean density of late-stage queen conch larvae at a nursery ground and the size of the benthic juvenile population in the subsequent year. The relationships are shown for nurseries in the Exuma Cays, Bahamas, and Florida Keys. Circles represent the larval collections for 1992 and juvenile surveys in 1993. Triangles represent larvae in 1993 and juveniles in 1994. Linear regressions and 95% confidence intervals are shown.

anism has been assumed for spiny lobster (*Panulirus* spp.) (Yeung and McGowan 1991) and postulated for queen conch (Berg and Olsen 1989, Mitton et al. 1989, Campton et al. 1991, Davis et al. 1993). Long-distance transport is well documented for a variety of marine molluscs (Scheltema 1971, Scheltema 1986).

Circumstantial evidence supporting the hypothesis that surface currents carry queen conch larvae from the Caribbean Sea to the Straits of Florida was provided in recent collections made in the Florida Current. In June 1993, a mean density of 8.1 veligers · 100 m^{-3} was found 35 km south of Delta Shoal (Stoner unpubl. obs.). All of the veligers collected were >1.0 mm SL and near metamorphic competence. This concentration is an order of magnitude higher than most values found within the Keys, and only one collection, made late in the spawning season at DS2, yielded a higher concentration of late-stage larvae. Given assumed (high) natural mortality rates in conch veligers, it is improbable that high concentrations of late-stage larvae originated in the adult-poor Keys environment, where newly hatched larvae are relatively uncommon. Support for the hypothesis that larvae drift from Cuba to the Florida Keys has been provided recently by the release of surface drifters along the north shore of Cuba (T. Lee pers. commun.). The drogues made direct paths from Cuba to Florida over several days. Under prevailing conditions, the Florida Current front is 10–20 km south of the reef tract, and exchange between the Keys and the current may be uncommon, as shown by the sporadic presence of late-stage larvae at Delta Shoal and Looe Key.

The Exuma Cays island chain is probably a more efficient system than the Florida Keys in maintaining high concentrations of conch larvae close to the island shelf and nursery grounds. During the summer, when conch spawn, winds are nearly always onshore (east to southeast), and the prevailing northwest current (6–12 cm · sec^{-1}) along the Exuma Cays has a significant onshore (cross-shelf) component (N. P. Smith pers. commun.). The larvae are then drawn onto the nursery grounds of the Great Bahama Bank through the island passes by strong tidal currents (Stoner and Davis 1997a). A net flow of water onto the Bank in the pass north of Lee Stocking Island has been observed (Smith and Stoner 1993), and larval concentrations are often higher in nursery areas than offshore near the spawning grounds (Stoner et al. 1992, Stoner and Davis 1997a).

The Relationship Between Larval Supply and Juvenile Populations

Although cause and effect are not established in a descriptive study, differences in larval supply measured in this investigation provide a plausible explanation for the observed differences in juvenile populations of queen conch in both the Florida Keys and the Exuma Cays. This is consistent with Connell's (1985) suggestion that population size will be correlated with recruitment at low recruitment densities. Similar patterns of spatial variation related to larval supply have been observed recently for coral reef fishes (Milicich et al. 1992, Doherty and Fowler 1994) and barnacles (Bertness et al. 1992).

Regardless of the exact source of late-stage larvae for Florida Keys nursery areas, the correlation between larval abundance and juvenile population size in Florida was very high, with just one point lying outside a nearly perfect linear expression. It now appears that ephemeral and small populations of queen conch that exist close inshore along the islands are limited by a general lack of larvae reaching these nursery grounds. Only one veliger (early stage) was collected north of Hawk Channel, where a westward flowing current (N. P. Smith, pers. commun.) may effectively bar the transport of larvae from local spawning grounds, all found along the reef tract.

The correlation between larval abundance and subsequent juvenile population size was also significant in the Exuma Cays, but the relationship was different from that observed in the Florida Keys in two ways. The correlation coefficient was lower in the Exumas, and the slope of the regression was much higher, illustrating that fact that deviation from a linear model of the relationship can vary both within and between sites.

Some of the deviation from the linear relationship among nursery stations in the Exuma Cays can be explained by differences in larval delivery rates. The density of larvae does not measure the actual availability of larvae to a site, and flow past the settlement substratum must be considered (Olmi et al. 1990, Yund et al. 1991). In relative terms, measurements of larval density underestimate larval supply to sites with high flows and overestimate supply at sites with low flows. For example, current velocities at the nearshore stations (CHB and NBC) were relatively low and both had juvenile populations falling below the regression line. Nurseries with the highest tidal current velocities (SR and CBC) had juvenile abundances above the regression line. Attempts to collect queen conch veligers in tube traps, which integrate the abundance of larvae reaching a site over time (Yund et al. 1991), have not been successful, even at station SR, where veligers were most abundant (Stoner unpubl. obs.). Undoubtedly, recruitment to the benthos involves a complex interaction of the density of potential settlers and the regularity and rate of their arrival.

The most remarkable difference in the relationship between mean density of late-stage larvae at a nursery ground and the subsequent juvenile population size in Florida and the Exuma Cays was the difference in slopes. Relatively similar mean densities of late-stage larvae were associated with very much higher juvenile populations in the Exuma Cays; the difference was as high as 40 times. Several explanations for this difference are plausible: (1) *Rate of delivery*—The most productive nurseries in the Exuma Cays are characterized by high current velocities (Stoner et al. 1994, Stoner et al. 1995), with much lower tidal velocities at the Florida Keys nurseries. (2) *Frequency of larval delivery*—Generally, the Exuma sites had higher frequencies of larval delivery to the nurseries than those in Florida, particularly in 1993. (3) *Size of the suitable nursery habitats*—In the Exuma Cays, habitats suitable to queen conch are large and typically have been below their carrying capacity for juvenile conch (Stoner et al. 1994, Ray and Stoner 1994). This provides a large potential settlement area for arriving larvae and may increase the actual numbers of larvae settling. Suitable nurseries in the Florida Keys are associated with relatively specific small backreef and nearshore habitats, more analogous to the small nearshore nurseries in the Exuma Cays (e.g., NBC and CHB) than to the large, open seagrass nurseries of the Great Bahama Bank (e.g., TBR, SR, and CBC). (4) *Settlement cues*—Recent experiments designed to test the response of late-stage queen conch larvae to natural cues from known nursery habitats near Lee Stocking Island (Davis and Stoner 1994) and in the Florida Keys (Stoner et al. unpub. obs.) have shown that settlement and metamorphic responses to sediments and macrophytes in the Exuma Cays are stronger than the responses to analogous substrata in the Florida Keys. Therefore, the frequency of settlement in the Florida Keys may be low. (5) *Postsettlement processes*—Growth and survivorship in the period after settlement can have a very large influence on the numbers of benthic juveniles animals in a benthic population (Keough and Downes 1982, Luckenbach 1984, Rowley 1989, Keesing and Halford 1992). Mortality rates in young queen conch are highly site specific and inversely density dependent (Ray and Stoner 1994). No comparable experiments have been conducted to compare mortalities between the two sites; however, the small size and low density of juvenile conch densities in Florida may prevent the safety in numbers observed in conch nurseries in the Exuma Cays. It is very likely that all of these mechanisms play at least some role in the low recruitment success of queen conch populations in the Florida Keys after 10 y of fishing moratorium.

Russ (1991) postulated that natural variation in spawning output directly affects local population size in most marine species because of high fecundities and broad dispersal capabilities. However, intense fishing pressure on fishes and invertebrates in the Caribbean has reduced the mean size and abundance of these species in many regions, and some self-recruiting systems with intensive local fisheries may be vulnerable to limitations related to reproductive output and larval supply (Munro et al. 1973, Munro 1983). Overfishing may, in fact, explain the apparent lack of recovery in Florida Keys populations. In the Florida Keys, adult conch populations were probably harvested to the point of recruitment overfishing by the mid-1980s, when a fishing moratorium was established. Today, the populations appear to depend on sporadic influxes of larvae from the Florida Current. If this form of recruitment is not effective in delivering a regular supply of larvae to the Florida Keys, the rehabilitation of queen conch stocks may depend on the success of hatchery rearing and the release of cultured juveniles. However, the limitations of releasing hatchery stocks are well known (Appeldoorn and Ballantine 1983, Jory and Iversen 1983, Stoner 1994, Stoner and Davis 1994).

Future studies will need to determine the relative significance of different larval sources in the Florida Keys and under what conditions larvae in the Florida Current can recruit to the Keys. Most important, species with pelagic larvae and high dispersal potential will need to be managed from the standpoint of metapopulation dynamics rather than on the basis of local populations (Farmer and Berg 1989, Fairweather 1991, Shepherd and Brown 1993, Man et al. 1995). Unfortunately, clear genetic markers have not been found for queen conch (Mitton et al. 1989), and other biochemical markers or new techniques are needed to identify stocks and stock sources. Models integrating oceanographic processes with larval production and behavior may provide another means of answering the important question of larval source. In any case, understanding larval recruitment processes and international cooperation related to spawning-stock maintenance will be crucial to the wise management of queen conch and other fishery resources in the greater Caribbean region.

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